AN ECOLOGICAL STUDY OF THE FLORA OF MOUNT WILSON

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PART IV. HABITAT FACTORS AND PLANT RESPONSE.

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1. Introduction.

The previous studies (Part i, 1924, Brough, McLuckie and Petrie; part ii, 1925, Petrie: Part iii, 1926, McLuckie and Petrie) of the vegetation of Mount Wilson have brought to light many interesting problems, the solution of which demands intensive study. The most outstanding feature of the vegetation of this region is the great contrast between different associations occurring in close juxtaposition: sclerophyllous Eucalyptus Forest alternating with Sub-tropical Rain Forest frequently and sharply in a comparatively small area. This condition has led us to make a more detailed enquiry into the habitat factors which are probably responsible for these remarkable distributional features, and the results of the investigation form the subject of the present communication.

Owing to the absence of a properly equipped permanent field laboratory, the scope of quantitative investigations was somewhat limited. From what has been done, however, it is possible to deduce, in a general manner, what are the basic factors controlling the distribution of the plant communities in this region, and to give an explanation of some of the remarkable features which were recorded in the previous papers. A number of more detailed observations are also recorded upon the ecological structure of the vegetation and upon the nature of its responses to the environment.

We have to record our indebtedness to Mr. D. J. Mares, Commonwealth Divisional Meteorologist, for rainfall and temperature data which have been utilized in this paper.

2. THE HABITAT FACTORS.

It is evident that in a small region like that under consideration, certain factors, e.g. climate, will be practically uniform throughout, and, although stamping their impress on the nature of the vegetation, are not directly the cause of the diversity of habitats within the region. Neither rainfall nor the general regional features of climate and season are variable to any marked extent at Mount Wilson. although it must not be thought that they are without their effect on the vegetation: but it is in other directions that one has to seek for the explanation of xerophytic and mesophytic associations existing side by side, and for the occurrence of Rain-Forest in a region with a rainfall rather below that of the typical habitat of that association-type. From what has already been written it will be clear that the edaphic factors, rather than the climatic, are of fundamental importance in producing the great differences in habitat which result in the presence of these two types; and it appears that we have here an example of compensating factors: in a region in which the climax association-type is sclerophyllous Forest, a local high edaphic favourableness apparently produces the same resultant as would a much higher rainfall with a poorer type of soil; so that a "post-climax", to use Clements's term (Clements, 1916), is here possible in the form of mesophytic Forest. It has also been made evident, however, that it is only in places where exposure is favourable that this effect is produced, so that exposure becomes a second factor of outstanding importance. It is therefore the edaphic factors, and the atmospheric humidity, which depends largely on exposure, that have claimed the greatest consideration in the present enquiry.

Among the general problems of distribution which it was hoped to elucidate are the following:

(1) The comparatively small amount of invasion of the basalt by types from the *Eucalyptus* Forests of the sandstone.

(2) The reason why the Rain-Forest grows equally well in the sandstone gullies and on the basalt caps.

(3) The absence from the basalt of certain Rain-Forest components in the sandstone gullies, such as *Callicoma*, *Todea*, *Blechnum capense* and *Histiopteris* incisa (see Part iii).

CLIMATE OF THE REGION.

Temperature.

No regular records have been taken at Mount Wilson, but the accompanying averages (Table i) of an eight years' record at Mount Victoria, which is only a few miles distant and is of approximately the same altitude, will give a sufficiently accurate conception of the nature of this factor in the region under study.

From these figures it is seen that the extremes are moderate; and although the summer months are fairly hot, the comparatively low minimum values in winter, and the occasional occurrence of snow, are undoubtedly of great significance in controlling the development of the Rain-Forest. We have described it as a luxuriant forest; yet it has not the tropical luxuriance of the more northern Rain-Forests. The floristic composition is comparatively limited, and there are only two dominants; whereas a tropical forest is characterized by great floristic variation. The structure is not excessively complex. The common features of a

Month.	Mean Maximum. Degrees Fahrenheit.	Mean Minimum. Degrees Fahrenheit.
January	74.7	53.6
February	73.3	54.3
March	68.6	51.0
April	61.7	46.3
May	53.8	41.6
June	48.4	37.3
July	41.6	35.2
August	51.6	37.0
September	58.8	39.6
October	65.4	44.3
November	71.5	48.0
December	74.9	50.6
Average for year	62.4	44-9

 TABLE i.

 Monthly Temperature Averages at Mount Victoria.

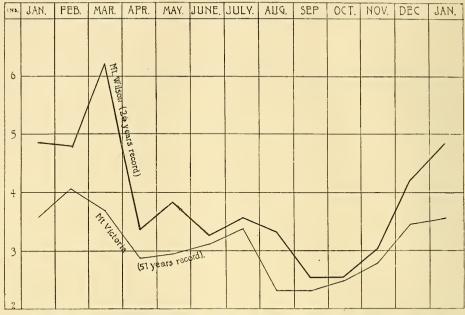
tropical Rain-Forest, *e.g.* very large leaves, plank buttresses, cauliflory, or epiphylly, such as are found even in the coastal forests of the same latitude in New South Wales, are practically absent. While epiphytic mosses and lichens are abundant, epiphytes of Pteridophytic and Angiospermic affinity are not profuse. Indeed, we are driven to realize that the luxuriant physiognomy of the Rain-Forest at Mount Wilson is imparted not by tropical structure and adaptation, but by its wealth of Pteridophytes and by its closeness of structure arising from high edaphic favourableness. Features such as these are in accordance with what one would expect in a montane sub-tropical or temperate Rain-Forest; and although the moderate rainfall is an important factor in causing them, there is no doubt that low temperatures in winter are also effective to a considerable degree.

Rainfall.

While the Blue Mountains as a whole have an average annual rainfall of 30 to 40 inches, Mount Wilson is exceptional in having the higher value of 46 inches. In Text-fig. 1 is given the monthly variation at Mount Wilson and also that at Mount Victoria, a more typical Blue Mountain area. It will be seen that not only is the rainfall at Mount Wilson higher than that at Mount Victoria throughout the whole year, but during the summer it is much higher: the maximum precipitation takes place during the hottest months, December to March.

This state of affairs is of considerable importance in connection with the occurrence of the Rain-Forest at Mount Wilson. While the basalt soil is the main factor leading to the development of this community on the plateau, there is no doubt that were it not for the high summer precipitation it would be a much less favourable habitat for the Malayan Rain-Forest types which at present characterize it. During the winter when desiccation is less, the smaller rainfall is not deleterious.

At Mount Victoria, although the maximum rainfall is also in the summer, it is not by any means so high; and this fact probably explains in part the



Text-figure 1. Annual rainfall graphs for Mount Wilson and Mount Victoria.

occurrence of Rain-Forest in shallow sandstone gullies at Mount Wilson which at Mount Victoria would probably be occupied merely by sclerophyllous *Eucalyptus* Forest.

The basaltic soil and the comparatively high summer rainfall then, are responsible for the maintenance of the luxuriant vegetation of the Mount Wilson area.

HUMIDITY AND EVAPORATIVE POWER OF THE AIR. Methods.

At the beginning of September, 1924, measurements were made of the evaporative power of the air in different habitats in order to obtain some knowledge of the requirements of the vegetation with regard to this factor.

As standard Livingston atmometer cups were unobtainable at the time, evaporimeters were made from Chamberland filter-candles attached to burettes by a piece of rubber-tubing, the whole being carefully filled with water so as to avoid the inclusion of air-bubbles. As it was desired to compare daily with nightly readings in the Rain-Forest to ascertain whether conditions bordering on saturation obtained there, burettes were used in place of the jars more commonly associated with the Livingston atmometer. This apparatus gave a rapid and accurate record of the water evaporated; it was found, however, during preliminary tests in the laboratory, that in a very humid atmosphere the presence of a column of water in the burette above the level of the filter candle resulted in a tendency towards exudation of water through the pores of the porcelain. To avoid this in all the evaporimeters used, the filter was raised above the level of the water in the burette by the insertion of a vertical piece of glass tubing between the filter and the burette. After this was done, and so long as the water in the burette was not above the level of the filter, trials in the laboratory showed that in an atmosphere of constant humidity the rate of evaporation was constant, and was not measurably affected by the level of water in the burette.

Shreve (1914, p. 43) has pointed out that atmometer readings taken in very dry and very moist climates are not strictly comparable, owing to a difference in the character of the evaporating water-film; and this objection would probably apply to our comparisons of readings taken in the *Eucalyptus* Forests with those in the Rain-Forests. The error, however, is not likely to be large enough to influence the general conclusions to be drawn from the results obtained.

The evaporimeters, although having approximately the same rate of evaporation, were standardized in the laboratory by comparison with the evaporation from an open water surface, whereby a factor was obtained for each evaporimeter. By this means the readings were standardized to the evaporation in cubic centimetres from an open water surface one square metre in area in which form they are expressed in the results given in Text-fig. 2.

Readings were taken early in the morning and at sundown for five successive days, the total evaporation for the twelve hours representing day or night being calculated therefrom. The total daily and nightly evaporation for the whole period is given for each station in Text-fig. 2.

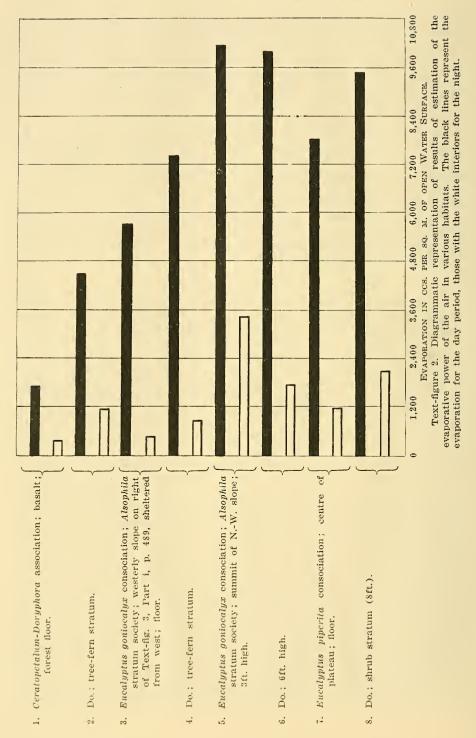
Discussion of Results.

This comparative study of the evaporative power of the air in different habitats gives an interesting confirmation of our observations upon the effect of the exposure on the distribution of the various communities.

The Rain-Forest, as we have previously stressed, is limited to the most sheltered habitats; and it is seen that the evaporative power of the air within it is very much less than in any other habitat. Water vapour appears to arise in considerable amount from the damp soil, forming a humid layer among the ferns on the floor of the forest. Owing to the deep shade and the extreme absence of wind in the forest, the moisture-content at the ground-level is high, and must border on, and no doubt at times attain saturation during the night. The greatly increased insolation at high levels in the Forest lowers the relative humidity and causes a striking difference between the values for the two strata expressed in the diagram. No such dissimilarity is noticeable in the more open communities, where there is little difference in the insolation of the various strata.

The Alsophila society of the Eucalyptus goniocalyx-E. Blaxlandi association has been described as much more tolerant of exposure, avoiding only the full brunt of the westerly winds on the open summits of the basalt caps, which are occupied by the Pteridium society in the E. Blaxlandi consociation (Part ii, p. 149). The results from stations 4, 5, and 6 show that the Alsophila society can withstand very high atmospheric dryness. The values in stations 5 and 6 are even higher than that in station 8 in the E. piperita Forest; and, although it is to be expected that more exposed westerly regions in the latter community would give higher values still, it is nevertheless evident that the series of increasingly mesophilous communities is not distributed in a series of habitats characterized by a correspondingly increasing atmospheric humidity. We are therefore led to suppose that the distribution of the Alsophila society is governed mainly by soil-moisture, and that it is very largely indifferent to exposure, except perhaps where it reaches an extreme on the open summits of the basalt caps.

The low values of the evaporation during the night periods are significant since the westerly wind prevalent during the day ceases in the evening.

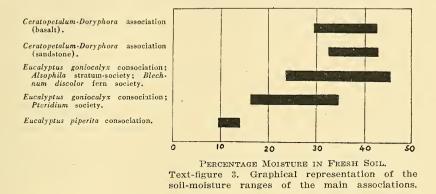


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THE MOISTURE-CONTENT OF THE SOIL.

A large number of samples of soil were collected at various times at Mount Wilson, in each case after a moderate spell of dry weather. These samples were passed through a 3 mm. sieve and the moisture content was then estimated by drying at 100° C.



The ranges for the values obtained for the soil-moisture of each association are given in Text-fig. 3. It must be understood that these ranges might possibly be found to be somewhat greater if samples were taken continuously throughout the year; they are nevertheless indicative of the striking features of difference between the habitats of the various communities.

From an examination of Text-fig. 3 it is seen how the range of soil moisturecontent for the Rain-Forests, whether on sandstone or basalt soil, does not vary beyond 13%. Thus, although a lower minimum may perhaps sometimes be reached, comparison with the ranges of the other communities at once suggests that the distribution of the *Ceratopetalum-Doryphora* association is determined by watercontent of the soil: the association as a whole is apparently independent of soiltype, so long as it finds the necessary high moisture-content. This view is supported by the occurrence of the Rain-Forest on other soils, *e.g.* shales, in other parts of the State.

The Alsophila society of the Eucalyptus goniocalyx consociation is not limited to the same extent by moisture-content, the values ranging from 45.2%near the Rain-Forest to 23.5% at the outer boundary; it is probable, however, that there is a minimum value for the lower extremity of the range (in the neighbourhood of 20%) for the habitat of this community, beyond which it is replaced by the *Pteridium* society. It may be asked why the high value of 45.2% is attained in this open community: the answer appears to be that the dense fern stratum may protect the soil from evaporation just as much as the Rain-Forest tree canopy. If then the soil is capable of holding this high percentage of moisture it would be expected that the *Ceratopetalum-Doryphora* Forest would be occupying the habitat; but, as we have seen, the exposure and the prevailing atmospheric humidity are not suited to the requirements of the Rain-Forest here, and in a strong westerly wind this high moisture-content no doubt decreases rapidly.

The *Pteridium* society appears to be one step further in the succession of the mesophilous to xerophilous communities; it is also noticeable that the *Eucalyptus* goniocalyx consociation is evidently confined to soils of a minimum soil-moisture

range, which, although low, is much higher than that of the *E. piperita* consociation.

The *E. piperita* Forest has the lowest values, and there is no doubt, moreover, that after periods of drought the minimum value would be even lower than that given. It is thus clear that the sandstone plateau is a highly xerophytic habitat. It is probable nevertheless that, since water drains rapidly downwards to the lower levels in sandstone soil, it does not have time to dry out between falls of rain, more especially as we have seen that the rainfall is fairly evenly distributed throughout the year.

The comparison of the soil-moisture values of this series of communities indicates clearly how the zonation of vegetation tends to coincide with a zonation of soil-moisture. There is no doubt that the falling gradient is increased by the progressive decrease in the capacity of the vegetation to conserve soil-moisture by shade and humus production. It appears then that the *Ceratopetalum-Doryphora*, *Eucalyptus goniocalyx-E. Blaxlandi*, and *E. piperita-E. haemastoma* var. *micrantha* associations are adapted to habitats of decreasing soil-moisture content: each will occupy the habitat where it finds its range, provided the other controlling factor of exposure permits; if this does not, one of the following associations in the series will occupy the habitat. The more xerophytic communities are no doubt excluded from the more mesophytic habitats by competition.

THE PHYSICAL STRUCTURE OF THE SOIL.

Samples of soil were taken at a depth of six inches from a number of typical habitats, and on arrival at the laboratory they were passed through a 3 mm. sieve. Two portions were then removed, the one being dried at 100° C. and ignited for the estimation of humus, the other being analysed mechanically by the method adopted by the British Agricultural Education Association (see appendix to Russell, 1921). The smaller separations, such as coarse and fine sand, were not made, as only the salient features of difference between the various soils were required. The results of these determinations are given in Table ii.

Discussion of Results.

Obviously the great difference in the physical structure between the basalt and sandstone soils will be a key to a number of other factors, since it will affect the aeration, moisture-retaining capacity, colloidal properties, etc., and will also be likely to have a marked influence on the root-systems. Aeration is one of the chief concomitants of the physical structure of a soil; and it is well known that sandstone, open and porous in nature, is abundantly ventilated and well drained, while clays, on account of the smallness of the component particles are poorly aerated and poorly drained, and tend to be infertile through lack of calcium carbonate. A priori it might be expected that the basalt, being a clay soil, although not deficient in calcium carbonate, might have an unfavourable influence on plant life on account of lack of aeration. Humus in amounts of 10% to 30%, however, as is present in the upper layers of the basalt soil (samples 1 to 8) counteracts the baneful effects of clay so far as low aeration goes, and renders the texture more open, without depreciating its moisture-retaining properties (Russell, 1921). This consideration probably explains the presence of the same association on the basalt slopes and in the sandstone gullies throughout this area -a distributional phenomenon which might lead one to deny the influence of edaphism on the distribution of vegetation. From this aspect of the humus-

TABLE ii.

Results of Mechanical Analysis of Soil Samples.

No. of Sample.	Community.	Habitat.	Fine Gravel.	Sand.	Silt.	Clay.	Humus.
1 2 3 4 5 6	Ceratopetalum- Doryphora association.	Basalt. Do. 1 ft. deep. Do. 5 ft. deep.	% 3·51 	% 21.06 	% 2·34 	60·32	$ \begin{array}{c} c_{\phi} \\ 13.77 \\ 19.04 \\ 26.45 \\ 19.04 \\ 10.40 \\ 12.11 \end{array} $
7	Eucalyptus goniocalyx consociation; Alsophila society.	Basalt.					30.25
8	Do. Tree-fern boundary.	Edge of basalt.				-	16.48
9		Ridges of N.E. slope below basalt.	8.67	68.15	9.97	2.97	10.24
10 11 12	Do. Pteridium society.	Sandstone; centre of plateau.	10.39 5.28	59·32 64·90	8·45 2·45	2·74 7·75	10.04 19.10 19.63
13	E. piperita consociation. Pteridium society.	Sandstone.	6.80	75.19	6.33	0.00	12.84
14		Westerly slope re- corded in Part iii, p. 108, where <i>Telopea</i> appears.	13.54	73.40	3.27	1.24	8.55
15	E. piperita consociation.	Same slope; sand- stone below basalt; floristic composition, Part iii, p. 108.	8.12	77.73	6.11	2.77	5.27
16 17 18		Centre of sandstone plateau.	4·22 13·73	73.01 60.65	$\frac{8 \cdot 82}{6 \cdot 26}$	5.50 0.00	8.48 7.01 19.88
19	Ceratopetalum- Doryphora association.	Sandstone.	1.80	70.58	2.66	9.32	15.64
20		Sandstone a little below basalt.	9.78	54.35	5.75	2.73	27.39

Except where otherwise stated, samples were taken from a depth of six inches.

Diameter of Particles in various Fractions. Fine gravel = above 1 mm.

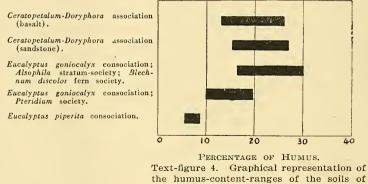
Sand	=	1-0.037 mm.
Silt	=	0.037-0.002 mm.
Clay	Ξ	below 0.002 mm.



content, which appears to counteract the effect of other components, the soils are perhaps not so fundamentally different in their influence on vegetation. Consequently it is not suprising that the actual number of plants with soil preferences were found to be very few (Part iii). Such preferences as appear to exist are probably in most cases the results of differences in properties of the soil solution.

Although the humus will have this striking effect near the surface, at depths of some feet its content in soils decreases rapidly, as is indicated in the present instance in samples 5 and 6, and eventually becomes quite low. At the same time the basalt soil is deep, since the rainfall is such as to cause rapid and penetrative weathering, and water and organic acids from the humus percolate through the soil and decompose the underlying rock. It is clear then that at greater depths the soil will not receive the beneficial effects of a high humus content; so that the vegetation would be expected to root in the upper regions if it is a type adapted to a well aerated soil. This point will arise again for discussion in a later portion of the paper.

The large percentage of clay and humus in sample 1 is plainly the key to the high moisture-retaining capacity, and consequent mesophilous vegetation, of the basalt soil. Probably, however, in the surface layers the humus is more important in this respect than the clay; for, as is usually the case, the moisturecontent closely follows the humus-content. Text-fig. 4 shows that the ranges of



the main associations.

these two properties correspond in a striking manner. It is thus the waterretaining capacity of the humus which makes it possible for the soil-moisture of the sandstone habitats clothed by Rain-Forest to be as high as those of the basalt, despite the absence of clay from the sandstone soil. It must be added, however, that the stations in the sandstone Rain-Forest from which samples were taken for moisture estimations were more particularly in the erosion channels occupied by *Dicksonia* and *Todea*, no samples unfortunately being taken from the apparently drier slopes devoid of tree-ferns; and, moreover, the Rain-Forest on the sandstone occurs only in valleys, where water is continually draining down from the highlands. In this connection it is interesting to note that, as was mentioned previously, the Rain-Forest at Mount Wilson occurs in gullies which on the other parts of the Blue Mountains would probably be occupied by a much more xerophytic community, since the water supply would not be sufficiently constant. In such habitats the gravitational water drains away rapidly and during a dry period disappears from the heights and so causes the gullies to become dried up. Hence the suggestion is offered that the water supply for the gullies at Mount Wilson is to some extent kept uniform and continuous by slow drainage from the basalt caps; owing to the low capillary power of such heavy clay soils the water would be conserved after rain and would be allowed to drain away slowly and uniformly, thus maintaining a constant supply for the gullies below.

This does not depreciate the previous statement that the humus is the main factor controlling the moisture-content of the soil, since these two factors are reciprocal: the formation of a water-retaining humus depends on the nature of the aspect and the vegetation allowing an accumulation of moisture in the soil: and were it not for this humus the water would probably dry out from the sandstone soil. The relationship between moisture-content and humus is probably responsible also for differences in the properties of the organic portion of the various soils. The moist volcanic soil and the moist and well-aerated and well-drained soil of the sandstone gullies must favour the production of a "mild humus", as in such habitats earthworms, fungi, and bacteria flourish; in particular the effect of earthworms is important since large species are abundant on the basalt and prove an important factor in ventilating the soil. On the other hand the dry sandstone soil forms a very different medium for the existence of these organisms, so that little humification goes on; in this case, therefore, although 7% to 8% of organic matter was found it is improbable that it would have the same moistureretaining capacity as that of the more humid habitats, and therefore is contributing to the xerophytic nature of the sandstone soil. This absence of humification in the habitat of the Eucalyptus piperita-E, haemastoma var. micrantha association adds point to its facies, as the bare patches between the individual plants are usually occupied by fallen leaves, twigs and branches, which in a more humid forest would soon rot away, but which here dry and accumulate until they provide material for the next forest fire.

A consideration of the analytical results shows that apart from the basalt there is no fundamental difference in the physical structure of the other soils. There is no evidence of mixing of the two main types except in the case of the basalt which contains a fairly high extraneous sand fraction, probably blown in by winds. The clay and silt fractions of the sandstone soils are largely composed of ferric oxide, a common mineral in the Hawkesbury sandstone, and which comes down with these fractions in the analysis. Samples such as 9 and 20 show that even on steep slopes there is no evidence of basalt soil being carried down very far and mixed with the sandstone, although there is no doubt that a mixture occurs in the ecotone region of the Rain-Forest referred to in Part iii (p. 98); the main erosion of the basalt, however, takes place in definite drainage channels, and has been described already (Part iii, p. 105).

In Part iii (p. 108) a description was given of the extension of the *Eucalyptus piperita* consociation to the basalt on a westerly slope. This spread is apparently only a small one, since the analysis of sample 14 shows that the *Lomatia* society is actually on the sandstone side of the junction, although from field observations we concluded that the soil was basalt.

The salient feature of this part of the investigation is the striking correspondence between the ranges of the moisture- and humus-contents of the soil. The clay fraction of the basalt soil holds sufficient moisture to provide a suitable substratum for the development of a rich humus, and is aided by shade and humidity in the Rain-Forest. This explains the mesophytic structure of the vegetation of the basalt soil, a vegetation which extends on to the sandstone only AN ECOLOGICAL STUDY OF THE FLORA OF MOUNT WILSON, IV.

on slopes or in valley floors which are damp through drainage. The predominant effect of the basalt soil on the distribution of the various associations depends almost solely upon its capacity for retaining water.

Up to this stage then we seem to have found two outstanding factors controlling the distribution of the plant associations. The first of these is *aspect*, which has both a direct effect on the vegetation through the atmospheric humidity, and also an indirect effect by influencing the evaporation of water from the soil. The second factor is the *moisture-content of the soil*, dependent on the humus, which in turn is dependent on the clay fraction of the basalt soil, upon drainage and upon shade.

THE HYDROGEN-ION CONCENTRATION OF THE SOIL SOLUTION.

On account of the high base-content of basalt soils, and the continuous filtering of water through it, it was thought probable that leaching would have an influence on the soil acidity; in any case the latter was likely to be a factor of interest in a region so marked as Mount Wilson in edaphic variation.

Clark and Lubbs' indicators were used for the estimations of the hydrogenion concentration of the soil. The procedure was based on Wherry's field-method (Wherry, 1920), with certain modifications: thus it was found necessary in the case of soils which remained turbid for a long period to filter them through ashless filter-papers, having carefully leached these until the washings gave a neutral reaction with brom-thymol blue; it was also found advisable to use the same quantity of water for each extract in order to obtain comparative results, a conclusion arrived at also by other workers (Wherry, 1924).

In Table iii are given the $P_{\rm H}$ values for samples taken at a depth of 6 inches from the various habitats. Each represents the results of a number of determinations from different parts of the community. The acidity was found to be practically uniform in these habitats at depths from 2 to 8 inches.

TABLE III.

Hydrogen-Ion Concentration of the Soil Solution from the Habitats of the Main Communities.

Ceratopetalum-Doryphora association; basalt				Р _н . 6·5-7·0
Eucalyptus Blaxlandi consociation; summit of basalt				
E. goniocalyx consociation; Alsophila society	• •			6.5
E. goniocalyx consociation; Pteridium society				
E. piperita consociation				
Ceratopetalum-Doryphora association; sandstone	••	••	••	6.5

The lack of variation in these results is a prominent feature. Despite the high content of bases, such as calcium, characteristic of basalt soil, the buffer action apparently prevents any fluctuation in the hydrogen-ion concentration of the soil solution. In all the soils except the dry sandstone the high content of colloidal material in the form of humus and also of clay in the case of the basalt, readily explains this buffer action; in the case of the sandstone it is to be presumed that the absence of an appreciable quantity of basic material on the one hand, and the absence of much humification or abundance of respiring root-systems on the other, mitigate any tendencies towards departure from neutrality in the soil-moisture.

From this it is clear that the hydrogen-ion concentration of the soil solution is not a factor of significance in the study of the distribution of the vegetation at Mount Wilson.

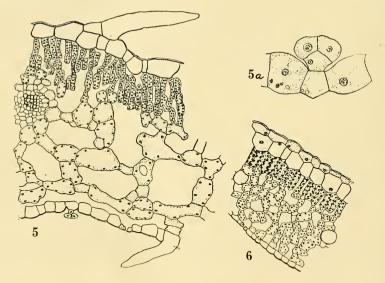
3. PLANT RESPONSE.

In preceding communications on the ecology of the Mount Wilson area. we have described the main features of the physiognomy and distribution of the flora and have endeavoured to interpret these as responses to certain factors or factor complexes of the environment. In the present paper we have endeavoured to analyse the environmental factors and to deduce the relative significance to the flora of each of the more important. We have indicated the outstanding differences in the various plant associations which occur throughout this area. and now furnish an account of the chief anatomical characters of the most important types of these associations. As Cannon (1924, p. 103) points out, two different and important groups of factors must be considered in the attempt to interpret the anatomical peculiarities of plants from the physiological point of view. namely heredity and immediate environment. The fact that different genera of the same family and even different species of the same genus attain to harmony with the environment by the most varied anatomical characters, seems to us to indicate that another set of influences of an hereditary nature is acting simultaneously with the present environment, and that the structure of the living types is, generally speaking, the result of the impress of two different categories of forces. On the other hand the physiologist knows on experimental grounds that certain characters are definitely plastic and modifiable by changing environment; hairiness may be replaced by glabrousness by cultivation in a more humid atmosphere; sclerophylly may be replaced by more mesophytic characters under similar conditions; nanism may give way to a taller habit; in short most of the characters of a highly xerophytic plant are changeable under a changed environment, provided it acts for a sufficiently long period during the development of the individual. The different "adaptations" of plants to the more xerophytic or mesophytic conditions appear to us to support the view that the present structure is the resultant of factors now operating but modified in certain respects by the cumulative influence of hereditary forces. This is all the more reasonable when we consider that members of the same family growing under precisely the same conditions in the same locality, show, amidst a general similarity of response certain individual differences. Speaking generally the types from the Ceratopetalum-Doryphora Rain-Forest (as the following descriptions will show) have thin unwettable cuticles, little or no sclerenchyma, stomata flush with the epidermis and without the outer vestibule characteristic of xerophytic types, poorly developed palisade and a great development of spongy mesophyll with large air spaces. The types from the Eucalyptus piperita-E. haemastoma association on the dry exposed sandstone habitat have stomata sunken in grooves or pits, hairiness, considerable sclerenchyma as hypoderma or as girders associated with the veins, strongly developed palisade and proportionately poorly developed spongy mesophyll, tannin deposits, enormously thick cuticles and outer epidermal walls, and frequently oil sacs.

In these xerophytic types the outer epidermal wall is generally heavily thickened owing to the deposition of anhydrides under the influence of the desiccating conditions. Strong cuticularization is a prevailing feature as the deposition of cutin is intimately associated with the transpiratory activity of the leaf. In the species of *Banksia* mentioned the stomata occur in pits, the cuticle of which is poorly developed. The stomata are usually sunk below the general surface of the leaf, and the cuticle forms, in many types, a prominent ridge overarching the guard cells, thus constricting the approach to them. Between these two extreme groups of structures are those displayed by components of the *Eucalyptus goniocalyx-E. Blaxlandi* association which develops on a much less xerophytic habitat than the *E. piperita-E. haemastoma* association. The anatomical characters common to these components of the associations at Mount Wilson may be seen more readily from the following descriptions and figures.

LEAF STRUCTURE OF THE CHIEF CONSTITUENTS OF THE Ceratopetalum-Doryphora ASSOCIATION.

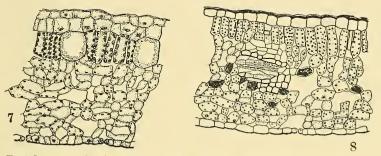
Fieldia australis. The chief characteristics are (a) the very thin cuticle for facilitating cuticular transpiration, (b) the poor development of palisade tissue owing to growth in a shaded environment, (c) the extensive intercellular space system of the leaf facilitating aeration and transpiration (the air channels being internal evaporating surfaces), (d) the poorly developed vascular tissue, (e) the numerous short hydathodes for secretion of excess water, and (f) the numerous stomata on the lower surface for aeration and passage of water vapour. These are structural features which characterize a type growing in a shaded moist environment, where aeration and transpiration require to be stimulated as far as possible by anatomical deviations from the normal type (Text-fig. 5, 5a). It has been shown earlier in the paper that in the lower strata of the Rain-Forest, which form the habitat of *Fieldia*, the atmospheric humidity is often in the neighbourhood of saturation.



Text-figure 5. Section of leaf of Fieldia australis. \times 115. Text-figure 5a. Hydathode of Fieldia australis. \times 300. Text-figure 6. Section of leaf of Atherosperma moschatum. \times 115.

Atherosperma moschatum. In this type the cuticle and outer epidermal cells are thin; the stomata are numerous and on the lower surface only. A hypodermal layer of relatively large clear cells is present on the upper surface, suggesting an aqueous tissue in structure; a narrow palisade layer is developed, while a loose spongy mesophyll occupies more than half the cross section of the leaf. The palisade layer contains relatively more chromatophores than the cells of the spongy mesophyll (Text-fig. 6).

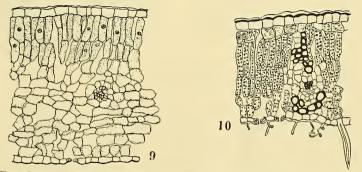
Doryphora sassafras also has a hypodermal layer of clear thin-walled cells devoid of chlorophyll and suggesting an aqueous tissue. This may be correlated with the fact that Doryphora frequently grows in more illuminated and drier situations than prevail in true Rain-Forest areas. The palisade layer is narrow with considerable spaces between certain cells, and large lysigenous oil-glands. The spongy mesophyll occupies more than half of the cross section of the leaf as in Atherosperma. The stomata are numerous and occur on the lower surface. The cuticle on both surfaces is thin (Text-fig. 7).



Text-figure 7. Section of leaf of Doryphora sassafras. \times 115. Text-figure 8. Section of leaf of Ceratopetalum apetalum. \times 115.

Ceratopetalum apetalum. There is no hypodermal layer below the upper epidermis as in *Atherosperma* and *Doryphora*, while the palisade layer is slightly more elongated in comparison with those types. The spongy tissue is extensively developed, while a few isolated tannin cells are distributed through it. A few comparatively thick-walled cells surround the vascular bundles. The cuticle on the upper surface is more strongly developed than in the previous types (Text-fig. 8).

Quintinia Sieberi. This is also a typical mesophyte which frequently starts development from seeds deposited on the trunks of treeferns etc. Compared



Text-figure 9. Section of leaf of Quintinia Sieberi. \times 115. Text-figure 10. Section of leaf of Callicoma serratifolia. \times 115.

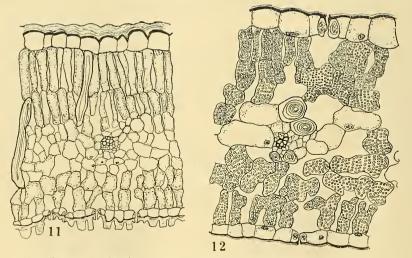
with *Atherosperma*, *Doryphora*, and *Fieldia*, the palisade is more strongly developed, although the proportion of palisade to spongy mesophyll is only very slightly different. Thick walled cells are absent from the smaller veins, while stomata are both numerous and flush with the other epidermal cells (Text-fig. 9).

Callicoma serratifolia occurs in water courses and drainage channels throughout the sandstone and consequently shows an anatomical structure intermediate between the mesophytes of the Rain-Forest and the xerophytes of the Eucalyptus piperita forest. The upper cuticle is much thicker than in Ceratopetalum. The hypodermal layer contains a tannin-like deposit, the palisade layer is better developed and occupies more than half of the cross section of the leaf. Air channels are extensive, stomata are numerous, and hairs are developed from the lower epidermis. Numerous thick-walled cells occur on the adaxial and abaxial surfaces of the vascular bundles. These are characteristics which stamp Callicoma as a form somewhat intermediate between the Rain-Forest Flora and the highly xerophytic individuals of the exposed sandstone habitat. (Text-fig. 10).

LEAF STRUCTURE OF THE CHIEF COMPONENTS OF THE Eucalyptus piperita-

E. haemastoma association.

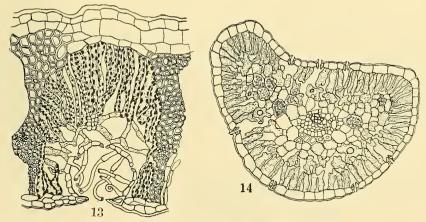
Telopea speciosissima. The upper cuticle is very thick and laminated, the outer epidermal wall is also thick, and the palisade tissue is composed of elongated cells occupying about half the cross section of the leaf; stereids occur



Text-figure 11. Section of leaf of *Telopea speciosissima*. \times 115. Text-figure 12. Section of leaf of *Persoonia salicina*. \times 115.

as strengthening cells both in the palisade and spongy mesophyll. The latter is composed of small cells in the centre and more elongated cells within the lower epidermis somewhat suggesting a palisade layer. The cuticle of the lower epidermis is very papillate and forms a cuticular ridge over the stomata which are sunk slightly beneath the other epidermal cells. A small outer and large inner vestibule occur in association with the guard cells—a character to be expected in a xerophytic sandstone type (Text-fig. 11). *Persoonia salicina* is an isobilateral type in which palisade tissue is developed on both surfaces, with larger air channels than might be expected in a xerophytic type. The leaf is thick and slightly succulent, and intensely green owing to the enormous chlorophyll content of the cells. The centre of the leaf is occupied by large colourless cells with mucilaginous sap, and cells with thick stratified mucilaginous walls. Isolated stone cells also occur. The guard cells are not so sunk as in *Telopea*, possibly owing to the vertical position assumed by the lamina through the twisting of the petiole through an angle of 90°. The cuticle is not nearly so thick as in *Telopea*, and forms a smooth layer on the surface (Textfig. 12).

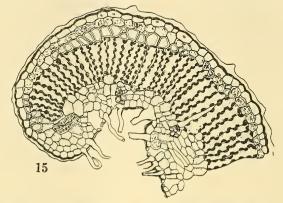
Banksia serrata is one of the most extreme xerophytic types in this association. The upper epidermis is covered by a very thick smooth cuticle; a hypodermis of two or three layers of clear cells probably represents an aqueous tissue. The palisade tissue is developed in relation to the cavities on the lower surface, and is composed of long narrow cells with large air spaces between them. The cavities occur at frequent intervals and are lined by epidermal cells, interrupted by raised stomata, and producing twisted hairs. Directly beneath the cavities there is developed a very loose network of mesophyll cells containing few chloroplasts compared with the palisade cells. The vascular bundles are strengthened by means of sclerenchyma extending as girders from one epidermis to another. The lower epidermis, excepting that of the cavities, is strongly cuticularized while a hypodermal layer of colourless cells is situated beneath the epidermis (Textfig. 13) (compare Hamilton, A. G., Aust. Ass. Adv. Sci., 1907, Adelaide, p. 484, 1908).



Text-figure 13. Section of leaf of *Banksia serrata*. × 115. Text-figure 14. Section of leaf of *Persoonia acerosa*. × 115.

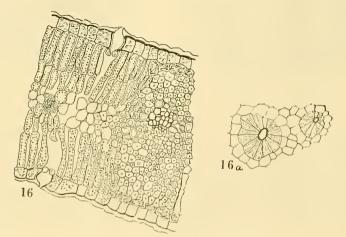
Persoonia acerosa. The cuticle of this pinoid type is fairly thick, and the guard cells are depressed at the base of the outer vestibule formed by the cuticular ridges. The palisade tissue is arranged concentrically within the epidermis. The centre of the leaf is occupied by the vascular bundle and by colourless cells, some of which contain starch, and others probably represent aqueous tissue. Isolated groups of sclerenchyma cells occur in the mesophyll, and in relation to the vascular bundles. The air space system is more elaborate than might be expected in a xerophytic type (Text-fig. 14).

Banksia spinulosa. In this type the leaf margin is recurved, and numerous slightly raised stomata occur in the cavity so formed. Hairs arise from the epidermal cells in the vicinity of the guard cells, which open into fairly large sub-epidermal chambers or cavities. Very little tissue of a spongy nature is developed, while about three-fourths of the cross section of the leaf is composed of elongated palisade cells with very narrow intercellular spaces. The cuticle is strongly developed on both surfaces, while the outer epidermal wall is thickened; the hypodermis is composed of deeply staining tannin cells and sclerenchyma. All the anatomical characters of this type confirm the xerophytic structure of the leaf to be expected from the habitat of the plant (Text-fig. 15).



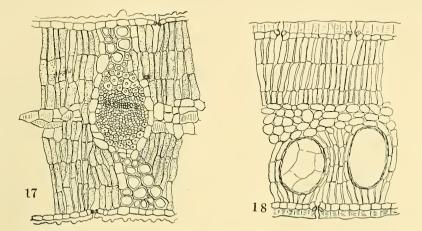
Text-figure 15. Section of leaf of Banksia spinulosa.

Hakea dactyloides is an isobilateral type with strongly developed palisade on both surfaces. The main bundles are surrounded by sclerenchyma developed as girders connecting the surfaces of the leaf. The centre of the leaf is occupied by colourless loosely arranged cells, while the stomata are deeply depressed and the ridges of the thick cuticle form comparatively large cavities above the guard cells. Many of the epidermal cells contain a deeply staining substance like tannin (Text-figs. 16, 16a) (compare Hamilton, A. G., PROC. LINN. Soc. N.S.W., 1914, p. 152).



Text-figure 16. Section of leaf of *Hakea dactyloides*. × 115. Text-figure 16a. Surface view of cuticular ridges overarching the guard cells. × 115.

Eucalyptus piperita has an isobilateral type of leaf, with compact palisade tissue and narrow air spaces. Stomata are found on both surfaces, while aqueous tissue occupies the centre of the leaf on each side of the main vascular bundles. Sclerenchyma is formed in association with the chief vascular bundles and forms a girder across the leaf. A layer of water-jacket cells is frequently present on each side of the vascular bundles. The cuticle is very thick, but the outer epidermal wall is exceptionally thin (Text-fig. 17).



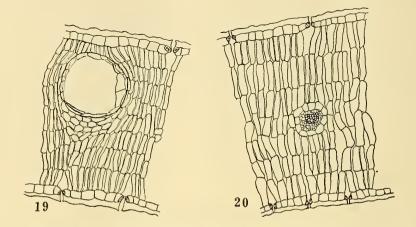
Text-figure 17. Section of leaf of *Eucalyptus piperita*. × 115. Text-figure 18. Section of leaf of *Eucalyptus haemastoma*. × 115.

Eucalyptus haemastoma resembles *E. piperita* in its isobilateral structure. The chief differences are in the greater development of the cuticle, and the definite central aqueous zone between the palisade of the lower and upper surface. The guard cells of this type like those of *E. Blaxlandi* are distinctly elevated, but protected by a well-developed outer vestibule formed by the enormously thick cuticle. The very narrow intercellular spaces and the consequent compactness of the palisade cells of this species are definite indications of the necessity of rigid control of the transpiring surface, both internal and external. The large proportion of oil glands in these two species may be regarded as an indication of their habitat being more xerophytic than that occupied by the species *E. goniocalyx* and *E. Blaxlandi* in which the glands are less numerous in the leaf (Text-fig. 18).

The components of the *E. piperita-E. haemastoma* association have adopted sclerophylly instead of succulence as their adaptation to the environment. The majority of the species are glabrous and strongly cutinized epidermal cells take the place of trichomes. Several of the species are isobilateral, and develop palisade tissue on both surfaces. The intercellular space system of the mesophyll is exceedingly variable; but generally speaking, types with strongly developed palisade tissue have relatively small and narrow intercellular spaces. In the spongy parenchyma of dorsiventral leaves the spaces are comparatively larger. Perhaps these features of the photosynthetic tissue may be correlated with the aridity of the habitat.

The structure of the foliage of the species of *Eucalyptus* from the various associations characterized generally by differences of environment, indicates some degree of correlation between the anatomical structure and the more important environmental factors, almost amounting to direct cause and effect.

In *E. goniocalyx* the palisade tissue is loosely arranged with numerous intervening spaces for aeration, while central aqueous tissue like that in *E. haemastoma* is generally absent, except in association with the vascular bundles. The cuticle and outer epidermal wall are not so extremely developed



Text-figure 19. Section of leaf of Eucalyptus goniocalyx. \times 115. Text-figure 20. Section of leaf of Eucalyptus Blaxlandi. \times 115.

as in *E. haemastoma*, but nevertheless they indicate a xerophytic type, despite the fact that it grows in a soil with a high water content. Owing to the height attained by the individual and the consequent high rate of transpiration due to exposure and the general evaporating effect of the atmosphere water control is very necessary (Text-fig. 19).

In Eucalyptus Blaxlandi the same structural features are revealed. As in E. goniocalyx, the guard cells of the stomata are practically flush with the other epidermal cells, or slightly raised and situated at the base of a cavity formed by the overarching cuticle (Text-fig. 20). In these two species of Eucalyptus the stomata are much more numerous than in the sandstone species, and taken as a whole the anatomical characters of their foliage stamps them as being types growing under much more favourable conditions of water-supply than E. piperita and E. haemastoma.

As compared with E. haemastoma and E. piperita the number of oil glands per unit area is less—a fact which might be interpreted as having some relation with the difference in the aridity of the habitat.

In *E. haemastoma* the colourless aqueous tissue forms a definite zone in the centre of the leaf between the abaxial and adaxial palisade.

Table iv gives the relative number of stomata in some of the chief components of the various associations:

Plant.	Ceratopetalum- Doryphora Association.	E. goniocalyx- E. Blaxlandi Association.	E. piperita- E. haemastoma Association.		
Eucalyptus goniocalyx E. Blaxlandi Alsophila australis Acacia melanoxylon Lomatia longifolia Drimys dipetala Pittosporum undulatum Blechnum discolor Dicksonia antaretica	Upper Lower Surface. Surface. (Isobilateral) (Isobilateral) (Isobilateral) 0 280 0 184 0 60 0 113	Upper Lower Surface. Surface. 33 109 184 188 0 99 236 246 0 205	Upper Lower Surface. Surface.		
Eucalyptus piperita E. haemastoma Persoonia salicina Telopea speciosissima Hakea dactyloides	(Isobilateral) (Isobilateral) (Isobilateral) (Isobilateral)		$\begin{array}{cccc} 60 & 107 \\ 81 & .81 \\ 24 & 28 \\ 0 & 184 \\ 134 & 140 \end{array}$		

TABLE iv.Stomata per sq. mm.

THE ROOT-SYSTEMS.

The relation of root-reaction and root-type to species distribution is a most important feature of ecological study, and yet, on account of the difficulty of investigation, it has been too much neglected. In the present instance, although no detailed drawings have been made, we are able to place on record some qualitative observations which have proved of interest.

The Rain-Forest of the basalt soil is characterized by the superficial rootsystems of all its components. The root development of the tree-ferns is meagre and shallow; that of the trees, although spreading broadly and considerably branched, is confined to a great extent to the first feet of the soil. This is clearly a reflex of the conditions of aeration as previously described: the lower layers are probably quite unfavourable for root-growth; at all events no types at Mount Wilson appear specially adapted to deep penetration in this soil.

In the sandstone Rain-Forests the root-systems of the trees may be somewhat deeper: upon this point our observations are incomplete. It is worthy of note, however, that *Callicoma serratifolia*, in exception to the other types, has a deeply penetrating root-system. This gives some insight into the absence of this type from the basalt Rain-Forests: if a deep root development is a rigid character, it is obvious that *Callicoma* could not grow on the heavy basalt soil without being suffocated.

Although this suggestion presents itself in the case of *Callicoma*, it has nevertheless, still to be explained why *Todea barbara*, *T. Fraseri*, *Blechnum capense*, and *Histiopteris incisa* occur in the Rain-Forest of the sandstone but not on the basalt; and it must be confessed that no satisfactory interpretation of this has been found. The following observations, however, are placed on record in the hope that they may be of use in subsequently arriving at the solution.

Todea barbara and Histiopteris in the Rain-Forest are mainly confined to rivulets; such rivulets have not been observed in the basalt Rain-Forests; but one specimen of Todea barbara was seen in a creek running over basalt soil in a Eucalyptus-Alsophila community on the south-eastern side of the plateau. Todea barbara will occur in creeks outside the Rain-Forest in highly isolated habitats on the sandstone; it has also been found, however, in deep shade under damp rocks where there was no trace of running water. It may be that the chemical composition of the soil solution has some influence on the distribution of these types, but this is a fact which still awaits intensive study.

The Eucalyptus piperita-E. haemastoma var. micrantha association of the sandstone is characterized by the extremely deep root-systems of most of the components. It has already been explained that there is probably a higher moisture-content in the lower strata of the sandstone soil, and it is now evident that the plants growing thereon penetrate deeply for the apparent purpose of obtaining this; the open texture of the soil permits them to do so without suffocation. By this means not only are the roots enabled to obtain sufficient moisture, but they escape from what is likely to be a high soil temperature in the upper strata during the summer season. This character is a common feature of these sandstone plants, as has been shown by Cannon (1924). The absence of these sandstone plants from the basalt, as in the case of *Callicoma*, is perhaps due to the character of the root-system: it may be that a deep root-system is a rigid character here, which, as Cannon (1915) has suggested, is often the case.

Observations on the components of the *Eucalyptus goniocalyx-E. Blaxlandi* association have not been made, but it has been found that *E. Blaxlandi* growing on basalt soil has a shallow root-system, a fact perhaps correlated with its preclusion from the dry sandstone.

On the whole, then, it appears that the character of the root-system is a significant factor in the distribution of the vegetation of Mount Wilson. In the physiological reaction to their environment the roots of the sclerophyllous sandstone types have had to penetrate deeply and this character seems to have eventually become rigid: the Rain-Forest types have found it better to exploit the superficial strata where they could obtain all the moisture and nutritive substances required. The different plants appear to be confined to those habitats to which their particular type of root-system is adapted.

4. THE ULTIMATE CONCEPTION OF THE VEGETATION OF MOUNT WILSON.

Few montane forest regions offer such a unique field as Mount Wilson for ecological study, provided as it is with two such widely different floras and with two such widely different habitats. The main basis for our study has, indeed, centred round the way in which these two floras have competed for the occupation of these two habitats, and the way in which they have reacted to the environmental conditions.

Superficial survey would suggest that in a region such as this with alternating basalt and sandstone, the geological formation must be the habitat factor of most outstanding significance; yet observations have disclosed the striking fact that distribution of the communities is not to be correlated with this but rather with the *edaphic water supply*. Apart from the role of humus in the determination of soil moisture-content, neither chemical nor physico-chemical properties of the soil appear to have any fundamental distributional significance, except in the case of several minor subordinate species. Given the climate and the moderately favourable summer rainfall such as they are, wherever the aspect is sheltered, and conditions, whether they be due to drainage or to the physical structure of the soil, permit the establishment of a permanent high edaphic moisture-content, Rain-Forest holds its own; wherever, on the contrary, the true climatic climax habitat conditions establish themselves on the dry and bleak sandstone plateau, the sclerophyllous *Eucalyptus* Forest has unchallenged sway; and wherever conditions are of an intermediate nature, transitional types of community are to be found.

As progression or retrogression appears to be the fundamental feature in the development of plant communities we regard the Rain-Forest as a vestigial remnant of a former vegetation of widespread range in eastern Australia, which, now faced in most parts with xerophytic conditions inimical to its survival, has retreated to such habitats as we have shown still to furnish it with optimum conditions. The xerophytic habitats provided by the elevation of the Blue Mountain Plateau of sandstone, favoured the advance of the xerophilous endemic Flora which now occupies the greater part of this formerly Rain-Forest-clad terrain. Yet, though the old Malayan Flora is securely entrenched in the most favourable mesophytic habitat at Mount Wilson, and though it can even displace the autochthonous element in changing habitats, still wherever the conditions become a little more extreme, *Eucalyptus* secures a footing; and, as through future ages the basalt hills are slowly carried away by the unceasing agents of geological denudation, the area of the Malayan Forest will shrink before the dominance of the autochthonous Flora.

Summary.

1. This paper is a study of the habitat factors, and an attempt to correlate these with the interesting distributional features of the vegetation of Mount Wilson.

2. An explanation of the small amount of invasion of the basalt by types from the *Eucalyptus* forests of the sandstone, and why the Rain-Forest grows as well in many sandstone gullies as on the basalt caps is given in this paper.

3. An analysis of the data of rainfall, temperature, humidity and evaporative powers of the atmosphere in the different habitats, of the hydrogen-ion concentration of the soil solution, of the moisture-content of the soil is made, and the relative significance of these factors upon the distribution and organization of the various plant communities is discussed.

4. The $P_{\rm H}$ value of the soil solution is proved to be an insignificant factor in the distribution of the vegetation at Mount Wilson.

5. The moisture content of the soil—affected by its humus content, by the component clay fraction, by drainage, exposure etc., is of the greatest significance as a controlling factor of the distribution throughout this area. The significance of aspect and moisture-content of the soil outweigh the effect of all other factors.

6. The response of the more important components to the habitat factors is discussed; the general development of the root system in the various habitats, and the structure of the photosynthetic organs are investigated and correlated with the environment.

7. The distribution of the communities throughout the Mount Wilson area is controlled by the edaphic water supply rather than by the nature of the geological formation. 8. The Ceratopetalum-Doryphora association is the dominant community in the most favoured habitats, e.g. on the basalt slopes, and in the sandstone gullies.

The sclerophyllous *Eucalyptus* forests, represented by the *Eucalyptus* goniocalyx-E. Blaxlandi and the *Eucalyptus* piperita-Eucalyptus haemastoma associations, are the climax communities wherever the environmental factors fall below the optimum required for the *Ceratopetalum-Doryphora* association, *e.g.* on the sandstone slopes and more exposed habitats of the area.

9. The Malayan exotic flora represented by the *Ceratopetalum-Doryphora* association is a mesophytic community which formerly had a very extensive distribution in New South Wales but is now preserved in sheltered valleys and on basalt residuals. Its present area will become smaller as the agents of denudation carry away the basalt caps of the sandstone.

Addendum.

Note on the occurrence of Eucalyptus amygdalina var. nitida.

Since the publication of the previous parts of this work *Eucalyptus amygdalina* Labill, var. *nitida* Benth, has been observed at Mount Wilson. It was found as an almost pure consociation of the *Eucalyptus goniocalyx-E*. *Blaxlandi* association on a south-westerly slope. *E. Blaxlandi* was occasional, and the usual stratum-societies of *Alsophila* and *Pteridium* were present.

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